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POINTS OF VIEW

OBJECTIVE SCIENCE OR EVOLUTIONARY SPECULATION?– A REPLY TO P. B. TOMLINSON

In the February 1984 issue of *Taxon* Tomlinson discussed in a single "review," two papers on stelar morphology and the primary vascular system: Beck, Schmid and Rothwell (1982) and Schmid (1982), published in the same issue of *The Botanical Review.* His comments refer almost entirely to the first paper, and are concerned largely with his reaction to our discussion and interpretation of his and the late Martin H. Zimmermann's work on the primary vascular system of monocotyledons. We wish to comment on several issues that he raised.

Tomlinson disagrees with our interpretation of the eustele as characteristic of all seed plants. He feels that we fail to take into consideration the enormous diversity of vascular systems among extant plants, but overlooks the fact that a major emphasis of our paper is the diversity, especially the internodal diversity, among steles (see pp. 759–785, 792–796, 809–815). We found nothing in this diversity, however, to restrain us from proposing a general, integrative, stelar theory that encompasses all seed plants.

Unfortunately, our interpretation of the stele of the monocotyledons as a highly modified eustele apparently led Tomlinson to conclude that we "take issue with the extensive analytical work on monocotyledons" of Martin Zimmermann and himself; and further, that we "challenge [their] enormous body of objectively assembled information . . . [on] monocotyledonous vascular systems." On the contrary, we praise their work and believe that the descriptive aspects that illuminate the pattern of vascular bundles in the stele are a very significant contribution. Our disagreement is only in Zimmermann and Tomlinson's interpretation of data. They suggested (e.g., 1972, p. 154) that "there are fundamental differences between dicotyledons and monocotyledons in their vascular systems which can be recognized in structural terms . . . ." In contrast, we interpret their data, and data from other sources, to support the hypothesis that the monocotyledonous vascular system is basically similar to that of the dicotyledons—indeed, that it is a highly modified eustele.

Tomlinson believes that the eustele, or more specifically, the vascular bundle sympodia of which eusteles are comprised, cannot be precisely defined in the absence of developmental studies. According to Tomlinson, "so long as 'vascular sympodia' remain unaccounted for as developmental entities, they remain imprecisely circumscribed and the eustele concept becomes difficult to refute." That is interesting in view of the fact that most of the studies on the pattern of the primary vascular system conducted during the second half of the twentieth century have been developmental studies. It is true that the precision with which such studies have been conducted has increased dramatically during the past two decades. By far the most significant studies are those of Philip R. Larson (e.g., 1975, 1976, 1979, 1980). Tomlinson regrets that we "virtually ignored the recent precise and integrative studies of Larson." But far from ignoring Larson's studies, we found in them the best evidence for some of the conclusions we reached. Indeed, it is Larson's elegant demonstration of sympodia, even at the early stage of procambial strand development, that, in our opinion, lends very strong support to the concept of the eustele. Larson's work was not only discussed or referred to in several places in our paper (pp. 711, 731, 784, 790, 792, 814), but also one of his figures was used to illustrate a typical eustelar system (p. 770).

Our conclusions are criticized because they are construed by Tomlinson to be speculation based on an abstract conception of the eustele. An essential element of the scientific method is the development of hypotheses followed by testing, possible exclusion or rejection, and then revision (see Platt, 1964; Popper, 1968). Of the two competing hypotheses regarding the nature of the primary vascular system of monocotyledons, that of Beck, Schmid and Rothwell (and also of Maze, 1977) is no less objective than that of Zimmermann and Tomlinson. Indeed, both are based in part on the same data set. Only after continued testing and the possible exclusion of one of these hypotheses shall we know which contributes more to the progress of science.

Let us consider further Tomlinson's viewpoint that his and Zimmermann's work is "objective

science" and ours "evolutionary speculation." This viewpoint, as elaborated in Tomlinson's "review," is a criticism not only of our paper, but also implicitly impugns the methodology of all of comparative morphology, paleontology and phylogenetic inference in which scientists use their understanding of homologies as a basis for drawing conclusions, or formulating hypotheses about evolution.

The deduction of homologies among the steles of seed plants is admittedly a perilous pursuit given the discrepancies that often occur between interpretations of shared structure and function on the one hand, and shared ancestry on the other. Within the constraints of our always incomplete data base, workers who investigate different facets of a problem (e.g., architecture of vascular systems within extant plants, or comparative architectures of extinct plants) will undoubtedly be impressed differentially by various subsets of the data. We do not assert that our approach is more valid in the pursuit of an understanding of the significance of vascular architecture than is that of Tomlinson and his coworkers. Neither is our approach less valid or scientific because, as paleontologists, we may employ somewhat different methods, obtain data of a different nature, or draw different conclusions. In reality the descriptive methodology employed by all of us is essentially the same. While the methodology of phylogenetic inference may sometimes be less empirical than the experimental method, it is no less rigorous or valid in testing hypotheses. Nor is it less scientific if approached with objectivity. No data set will preclude the conscious or unconscious reaching of prior conclusions if one has not analyzed it objectively (Gould, 1981). Nor will the experimental analysis of inadequate and/or inappropriate data further scientific understanding.

Tomlinson intimates that our interpretation of the steles of monocotyledons as highly modified eusteles resulted from an attempt to support prior conclusions; but such a supposition does more to advertise a lack of appreciation for paleontological methodology than to call to question the validity of the interpretation. Our interpretation grew out of our understanding that members of a clade share similar genomes derived from common ancestors, and also are limited in their mature structure by the common constraints of developmental pathways. If uniform plant architectures were more important in the evolution of vascular systems than similar genomes, as Tomlinson seems to suggest, then one would expect to find little resemblance between the vascular systems of closely related plants with different growth habits. Conversely, close structural and developmental similarities among only distantly related plants would lead to similar vascular architectures. However, if one examines plants that conform to the same morphological model as established by Hallé and Oldeman (1970), it is clear that this is not the case. For example, as elaborated by Hallé, Oldeman and Tomlinson (1978), some dicots, monocots, tree ferns and cycads conform to Corner's model (pp. 109–118 of Hallé et al., 1978). Using anyone's classification and terminology, those from different clades (i.e., ferns and seed plants) have steles that are significantly different. On the other hand, plants of divergent growth habits from the same clade commonly have similar vascular architectures (Beck et al., 1982).

While the philosophical approaches we employ in our efforts to understand the fossil record may be, sometimes of necessity, different from those of neontologists, there is no question that paleontological investigations have contributed some of the most significant data for a better understanding of the structure and evolution of vascular plants. They will continue to do so into the indefinite future, differences of interpretation notwithstanding.

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ON THE REIFICATION AND DEIFICATION OF THE STELAR CONCEPT—ADDITIONAL COMMENT ON TOMLINSON

Tomlinson (1984) in his "review" of our papers (Beck, Schmid and Rothwell, 1982; Schmid, 1982—references above; the unqualified pages below refer to these two papers) has charged that our "ultimate reification" of the stelar concept "is detrimental" "to progress of our understanding of vascular systems in plants." The above rebuttal to Tomlinson attempts to demonstrate that our concern with "comparative phyletic analysis" and the stelar concept is no more of a "reification" than any other scientific hypothesis, including ones derived from a concern with "morphogenetic patterns," "developmental aspects," "completely reproducible methods," "objective science," and "experimental science" (all quotations from Tomlinson). Had we really wished to reify and/or deify the stelar hypothesis, we would have called it the "stelar theory" and not the "stelar concept." As elaborated on p. 698 of our paper, we explicitly declined the former expression and, in fact, departed from historical tradition in so doing. Throughout both papers we consistently used the expression "stelar concept," only occasionally using (e.g., p. 714) "stelar hypothesis," and then largely for stylistic variety. Van Tieghem and Douliot (1886a, 1886b), it might be noted, used none of these expressions, contrary to Tomlinson's statement that they are "credited with originating the '*stelar theory*'" (emphasis mine).

Most of Tomlinson's remarks dealt with the Beck et al. (1982) review rather than with the Schmid (1982) one and thus are addressed in the above rebuttal. However, a few of Tomlinson's comments impinging directly on my paper require comment here.

Tomlinson rightly noted that "complex stelar systems are accommodated with difficulty" in my classification of stelar types (pp. 700–701 and its elaboration on pp. 850–909). My categories of "polycyclic solenostele" and the coordinate "polycyclic dictyostele" were broadly defined (pp. 700, 861, 864) to include those situations where the cyclic arrangement is obscured (see especially p. 901), just as was the comparable category of "polycyclic eustele" (pp. 701, 867). Were I to redo the tabular "Classification of stelar types" in Beck et al. (1982) and Schmid (1982), I would more extensively and accurately define the former two types in a manner similar to "polycyclic eustele," that is, "with two or more concentric vascular cylinders, or else with a main vascular cylinder with internal or external bundles in a scattered or dispersed arrangement (as seen in transverse section); stele typical especially of those axes with a medullary or cortical vascular system, or both."

Cyathea fulva, which Tomlinson mentioned on the basis of Adams's (1977) exemplary and detailed study, has a stelar system with internal bundles in a scattered or dispersed arrangement. Its "polycyclic dictyostele" is similar to those of other species of *Cyathea* mentioned by Ogura (1972) in his review. Hence I did not reference *C. fulva* (Adams, 1977) and many other taxa, largely to keep my 19-page bibliography within manageable limits. Incidentally, in view of Tomlinson's unmitigated denegation